



Salicylic Acid Seed Priming Enhances Germination and Seedling Growth of *Lallemantia iberica* Under Mannitol-Induced Drought Stress

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ABSTRACT

Here, the potential effects of salicylic acid (SA)-assisted priming on the germination and seedling growth of *Lallemantia iberica* (cultivar Sara) under drought stress was assessed using a factorial experiment based on a completely randomized design (CRD) with three replications. Salicylic acid (SA) pretreatment was used at four levels (control (zero), 1, 2, and 3 mM) and drought stress was induced using mannitol at two levels (zero and 100 mM). The results showed that the interaction effect of salicylic acid pretreatment with drought stress was statistically significant ($p < 0.01$). High levels of drought stress (100 mM) caused a significant reduction in germination speed, shoot length, shoot weight, seedling dry weight, and relative water content. The highly significant positive correlation between root length and fresh weight (0.946**) suggested that longer roots are associated with greater fresh biomass. The results of the heatmap analysis provided a clear classification of treatments into two distinct groups in terms of the incidence or absence of mannitol. The results of the PCA provided insight into the morpho-physiological responses of *L. iberica* under drought conditions during seed germination, particularly when primed with the stress hormone of SA. The first two components of the analysis accounted for an impressive 91.5% of the total variation in the studied traits. However, pretreatment with SA (3 mM) increased the traits related to germination and seedling growth under drought-stress circumstances compared to stress conditions without SA pretreatment. This indicated that the use of SA pretreatment can mitigate the effects of drought stress on the Balangu plant during seed germination and seedling growth.

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1. Introduction

As agriculture is a crucial sector in Iran's economy, drought stress is a significant threat to food security, crop production, and rural livelihoods (Garshasbi, 2014). The negative impacts of drought stress on seed germination, such as limited water uptake and disruptions in enzyme activity and hormonal regulation, have been extensively studied in previous investigations (Ai *et al.*, 2024; Saha *et al.*, 2022). To address this issue, it is essential to understand the causes, effects, and potential solutions for drought stress in Iran. This understanding will assist in the development of sustainable water management strategies and agricultural practices (Yazdi *et al.*,

2022). However, an alarming fact is that nearly 74% of Iran's land area receives less than 200 mm of rainfall annually, with only about 10% occurring during the hot and dry seasons, as shown in Fig. 1. Furthermore, 52% of the country's annual rainfall and snowfall is concentrated in just 25% of its land area, leaving the remaining regions vulnerable to drought and potential crises in the near future, as identified by Garshasbi (2014).

In 2024, extreme drought conditions were experienced by almost 8% of the global land area, setting a new record (Blunden and Boyer, 2024). Therefore, addressing drought stress in Iran is not only crucial for the country's agricultural sustainability, but

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it is also critical for global food security and fighting against climate change.

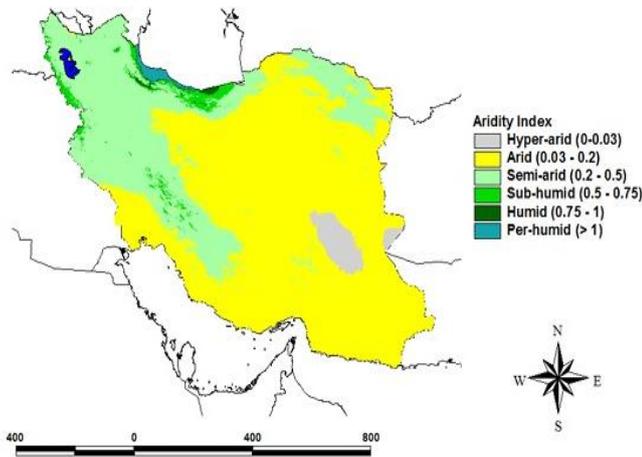


Figure 1. Aridity classes in Iran (Garshasbi, 2014).

Seed germination is a foundational process for plant growth and is particularly vulnerable to water scarcity. By studying how drought affects the germination process, we can develop effective strategies to promote crop resilience and mitigate the undesirable effects of water deficiency on plant growth. As highlighted by Lu et al. (2022), this knowledge is crucial for ensuring sustainable and secure food production in the face of changing environmental conditions. Seed priming has been developed as a highly effective agronomic tool that has the potential to revolutionize the agricultural industry. Through the process of seed priming, water uptake is improved, metabolic processes are activated, and stress resistance is enhanced. These benefits make it possible for plants to overcome unfavorable environmental conditions such as drought, high salinity, and extreme temperatures (Chakraborti et al., 2022; Saha et al., 2022; Aswathi et al., 2022). Additionally, the use of various priming materials such as Salicylic Acid, Gibberellic Acid, Hydropriming, Osmopriming, Biopriming, and Hydrocolloids has been extensively studied and proven to be beneficial in enhancing germination of the seeds and subsequent growth of the resultant seedlings, especially under serve unfavorable environmental conditions (Ellouzi et al., 2023; Marthandan et al., 2020). By enhancing seed vigor and increasing stress resistance, seed priming can greatly contribute to overall crop growth and yield (Ibrahim, 2016; Jisha et al., 2013; Bhanuprakash and Yogeasha, 2016).

The task of enhancing drought tolerance in Balangu (*L. royleana*) genotypes poses numerous difficulties, such as limited selection efficacy, the intricate nature of various biological factors, and the insufficiency of evaluation techniques for identifying desirable genotypes in breeding programs (Shams et al., 2022; Ahmadi and Omid, 2019). However, despite these challenges, the resilience of Balangu in harsh environments serves as a testament to the criticality of identifying and selecting genotypes with the ability to flourish in dry soils while still yielding significant crop output. This highlights the pressing need for innovative and effective strategies to overcome the barriers hindering the identification and incorporation of drought-tolerant Balangu genotypes in breeding programs, thereby contributing to the overall cultivation of more robust and productive crops. Previous studies have demonstrated the effective use of mycorrhizal fungi, humic acid, and putrescine treatments in alleviating the adverse effects of drought stress on *Lallemantia royleana*, leading to enhanced growth traits and improved phytochemical properties (Vakili et al., 2024). Furthermore, the application of salicylic acid has proven effective in enhancing drought resistance in *Lallemantia iberica* by improving physiological responses and grain yield under water deficit conditions (Naservafaei et al., 2025). The phytohormone of salicylic acid (SA) plays a vital role in managing growth and defense responses and has been widely studied for its potential role in seed priming. Earlier investigation indicated its ability to improve germination and stress tolerance, particularly in drought conditions, by stimulating metabolic processes, improving water uptake, and protecting seeds from oxidative damage (Hara et al., 2012; Imran et al., 2024).

The critical role of SA in response to drought stress has been extensively investigated in recent studies (Abdelaal et al., 2020; Khalvandi et al., 2021). SA has been found to induce and regulate various physiological and metabolic processes, including seed germination, leading researchers to explore its potential as a means of improving germination characteristics under drought conditions. For instance, Paravar et al. (2024) investigated the effects of SA seed priming on the germination properties of *L. royleana* under drought stress induced by PEG 6000 and found that SA priming had a positive influence on germination

parameters. Similarly, a study by Rafiq et al. (2021) examined the SA priming impacts on seed germination under drought stress made by polyethylene glycol (PEG) and discovered that SA priming at 225 ppm meaningfully enhanced germination rates and seedling vigor. Furthermore, the SA priming effect has been recently studied on the seed germination and seedling growth of sorghum under drought stress research, confirming its positive effect on improving germination and seedling emergence (Zhang et al., 2023).

The current study aims to examine the potential effect of SA priming on the seed germination and seedling growth of Balangu under drought situations. To the best of our knowledge, no previous studies have examined the effects of mannitol-induced drought stress on this particular genotype. As a result, the significance of this study lies in the evaluation of physiological and morphological responses during the germination stage of the Sara cultivar to osmotic stress caused by mannitol, bringing new and original findings to the existing body of knowledge in this field.

2. Materials and methods

2.1. Seed preparation

The freshly prepared seeds of *L. iberica*, Sara cultivar were prepared from the Dryland Agricultural Research Institute, Sararood Branch, Kermanshah province. The information related to this cultivar is available at the Seed and Plant Certification and Registration Institute. Details characteristics of this cultivar are shown in Table 1.

Table 1. The registered specifications for *L. iberica*, Sara cultivar

Specification	Details
Common name	Balangu-e-Shahri
Scientific name	<i>Lallemantia iberica</i>
UPOV code	LALLE_IBE
Cultivar name	Sara
Breeder	DARI (Dryland Agricultural Research Institute)
Cultivar owner	DARI (Dryland Agricultural Research Institute)
Year of introduction	2020
Cultivar code	1.6.3.1

2.2. Seed priming, mannitol-assisted drought stress induction and germination process

The study aimed to investigate the impact of SA priming on the seed germination and seedling growth of the Balangu (*L. iberica*), cultivar Sara. The

experiment was designed in a factorial pattern with three replications, arranged in a completely randomized design at the Agricultural and Natural Resources Research Laboratory in the Faculty of Agriculture at Razi University in 2024. The treatment factors consisted of four levels of salicylic acid (0, 1, 2, and 3 mM) and two levels of drought stress induced by mannitol (0 and 100 mM). Before the application of salicylic acid priming, the seeds were sterilized using a 2% sodium hypochlorite solution. Afterward, the seeds were subjected to the desired salicylic acid solutions and incubated under darkness at 4°C for 24 h, following which they were dried at room temperature. Subsequently, 15 seeds were placed in each 9 cm glass Petri dish on a Whatman cellulose filter paper, and a solution of 5 mL drought stress was added. The Petri dishes were then incubated at a constant temperature of 25°C. Seed germination was determined based on a radicle length of 2 mm (Causin et al., 2020). The number of germinated seeds was recorded daily. Furthermore, the weight of the seedlings was measured by drying the samples in an oven at 70°C for 24 hours.

2.3. Calculation of germination-related metrics and seedling growth parameters

In this study, the germination speed (GS) was calculated using Equation 1 (Bewley and Black, 2013).

$$(1) \quad GS = n / \sum t$$

where: n is the number of seeds that germinated at each count, and t is the time (in hours or days) after initiation of the germination test. Shoot and root length (mm), fresh and dry weights of shoot (mg) and seedling dry weight (mg) were measured after drying at 65-70°C for 48 hours. Relative water content (RWC) was measured using Equation 2 (Munns and Tester, 2008).

$$(2) \quad RWC = (FW - DW) / (TW - DW) \times 100$$

Where FW, DW and TW represent the fresh weight, dry weight, and turgid weight of the sample, respectively.

2.4. Statistical analysis

To analyze the data gathered, ANOVA analysis was conducted using the R software. To further explore the relationship between variables, Duncan's multiple range test was applied to compare mean values

($p < 0.05$), as a valuable tool to make robust and precise statistical inferences (Nasiri et al., 2025). To provide a comprehensive representation of the data, a Principal Component Analysis (PCA) was performed alongside heatmap visualization using the ClustVis web tool (Metsalu and Vilo, 2015). Additionally, a pairwise correlation analysis was calculated utilizing the R software, allowing for a more comprehensive understanding of the different traits and their relationships. This analytical approach provided a deeper understanding of the data, allowing for the identification of patterns and trends that may have otherwise gone unnoticed. The use of both ANOVA and PCA techniques showcases the thoroughness and rigor of the research, and the inclusion of heatmap visualization and pairwise correlation analysis adds a visual representation and further insight into the data. Overall, these analyses were integral in uncovering meaningful insights and drawing well-supported conclusions from the data.

3. Results and discussion

3.1. Effect of salicylic acid seed priming on the germination parameters of *L. iberica* under mannitol-induced drought stress

The ANOVA results (Table 2) at the germination stage of the *L. iberica* plant indicated that all studied traits exhibited highly significant differences at the 1% statistical level. This suggested a strong genetic or environmental influence on key germination parameters, including germination speed, root length, shoot length, FW, DW, and RWC. The significant variation observed in germination speed implies that different conditions or genetic backgrounds contribute to the rapidity of seedling emergence. A faster

germination speed is generally favorable, as it can enhance seedling establishment and early growth, potentially improving the overall vigor of the plant. The significant differences in root and shoot length suggest variability in the early developmental processes of *L. iberica*. Root length is particularly important for nutrient and water uptake, whereas shoot length determines the ability of the seedling to access light. The variations in these traits could be influenced by genetic factors or external environmental conditions such as temperature, moisture, and soil composition. The highly significant differences in fresh and dry weight indicate that biomass accumulation varies considerably among the studied samples. The FW reflects immediate physiological conditions, while DW represents the long-term biomass accumulation and energy storage capacity of the plant. This variation might be linked to differences in metabolic efficiency, resource allocation, and overall seedling health. RWC, a key parameter of water status and drought tolerance in plants, also exhibited significant variation. This suggested that different samples of *L. iberica* may have varying capacities for water retention, which could influence their resilience to water stress conditions. Additionally, the effects of SA, mannitol, and their interactions were found to be highly significant at the 1% probability level for all traits. This indicates that these treatments play a crucial role in influencing germination and early seedling growth. SA is supposed to be contributed to plant defense mechanisms and stress responses, while mannitol is often used to simulate osmotic stress conditions. Their significant effects suggested potential applications in improving germination performance under different environmental conditions.

Table 2. Analysis of variance of the SA seed priming effect on germination traits of *L. iberica* under drought stress

S.O.V.	df	Mean of Square					
		Germination speed	Fresh weight	Dry weight	Shoot length	Root length	Relative water content
Salicylic acid (SA)	3	74.87**	29.33**	0.94**	13.513**	216.86**	11.88**
Mannitol (M)	1	678.41**	624.25**	1.5**	442.90**	3335.39**	493.13**
SA × M	3	79.57**	35.64**	2.94**	3.75**	286.51**	113.17**
Error	12	6.98	0.81	0.16	0.71	1.91	7.012

**Significant at 1% probability level.

The mean comparison results based on Duncan's test (Table 3) provide valuable insights into the impacts of SA and mannitol treatments on the important germination and growth traits of *L. iberica*. The

maximum germination speed was detected in the treatment with 3 mM SA and 0 mM mannitol (67.29%), whereas the lowest germination speed was recorded for the combination of 1 mM SA and 100 mM mannitol

(Table 3). This indicates that SA at higher concentrations can enhance germination under non-stress conditions, but its effect diminishes when combined with high levels of osmotic stress induced by mannitol.

In terms of FW, the control exhibited the maximum value (29.2 mg), whereas the lowest value (12.2 mg) was recorded for the 3 mM SA + 100 mM mannitol treatment. This pattern emphasized the negative influence of high osmotic stress on seedling growth, which is further exacerbated by higher SA concentrations. For DW, the maximum magnitude (4.33 mg) was found in the control (0 mM SA + 0 mM mannitol), while the minimum value (2 mg) was observed in the treatment of “3 mM SA + 0 mM mannitol. This suggests that SA at high concentrations might hurt biomass accumulation in the absence of osmotic stress. Regarding root length, the longest roots (51.66 mm) were observed in the control group, while

the shortest roots (13.8 mm) were recorded for the 3 mM SA + 100 mM mannitol treatment. This indicates that root development is highly sensitive to osmotic stress, and high concentrations of SA do not mitigate this negative effect. The highest shoot length (14 mm) was observed in the 1 mM SA + 0 mM mannitol treatment, while the lowest shoot length (2.33 mm) was found in the 0 mM SA + 100 mM mannitol treatment. These results suggest that a moderate concentration of SA (1 mM) might promote shoot elongation under non-stress conditions, while high osmotic stress severely restricts shoot growth. Moreover, the highest and lowest RWC values were recorded as 93.26% in the control treatment and 75.23% in the 0 mM SA + 100 mM mannitol treatment, respectively. This highlights the severe impact of osmotic stress on cellular water retention, emphasizing the importance of maintaining optimal hydration levels for seedling survival and growth (Rivas-San Vicente and Plasencia, 2011).

Table 3. The effect of SA seed priming on some germination-related parameters and seedling traits of *L. iberica* under drought stress.

Treatment	Germination speed (%)	Dry weight (mg)	Fresh weight (mg)	Root length (mm)	Shoot length (mm)	Relative water content (%)
SA0mM + M0mM	58.44 ^{bc}	4.33 ^a	29.2 ^a	51.7 ^a	9.40 ^c	93.26 ^a
SA1mM + M0mM	56.38 ^c	2.33 ^{bc}	20.7 ^c	21.7 ^c	14.00 ^a	88.71 ^{ab}
SA2mM + M0mM	62.95 ^{ab}	3.00 ^b	23.8 ^b	42.3 ^b	11.93 ^b	87.35 ^b
SA3mM + M0mM	67.29 ^a	2.00 ^c	28.6 ^a	43.91 ^b	13.93 ^a	93.00 ^a
SA0mM + M100mM	57.86 ^c	2.00 ^c	17.6 ^d	16 ^{de}	2.33 ^e	75.36 ^c
SA1mM + M100mM	46.43 ^e	2.33 ^{bc}	15.3 ^e	17.7 ^d	4.53 ^d	84.68 ^b
SA2mM + M100mM	47.00 ^{de}	2.00 ^c	16.4 ^{de}	17.8 ^d	4.47 ^d	87.79 ^b
SA3mM + M100mM	51.24 ^d	2.67 ^{bc}	12.2 ^e	13.8 ^e	3.57 ^{de}	78.23 ^c

Data with the same letters in each column are not significantly different at $p < 0.05$ (Duncan's test).

3.2. Correlation analysis among studied traits

The results of the correlation analysis conducted among the studied traits (Fig. 2) revealed several significant and highly significant positive correlations. Specifically, fresh weight showed a substantial positive association with dry weight (0.795^{*}) and root length (0.946^{**}).

In addition, shoot length was found to have a significant positive correlation with fresh weight (0.755^{*}), and there was also a noteworthy positive correlation between dry weight and biomass, reflecting an overall increase in plant vigor and biomass accumulation (Xu et al., 2018). This trend is consistent with findings in other plant species and supports the notion that fresh and dry weights are positively correlated. Furthermore, the highly significant positive correlation between root length and fresh weight (0.946^{**}) suggests that longer roots are associated with

greater fresh biomass, consistent with studies in rice where root length and root weight have been found to positively correlate with plant yield. Similarly, the significant relationship between shoot length and fresh weight (0.755^{*}) suggested that taller shoots contribute to increased fresh biomass, as observed in studies on wheat seedlings. These correlations highlight the importance of root and shoot development in supporting overall plant vigor and biomass. The significant positive correlation between dry weight and root length (0.728^{*}) further emphasizes the key role of root systems in promoting above-ground growth, as evidenced in research on maize under various irrigation conditions (Shahzad et al., 2023). Overall, the results of this correlation analysis provide valuable insights into the relationships among key traits and their contributions to plant growth and biomass accumulation.

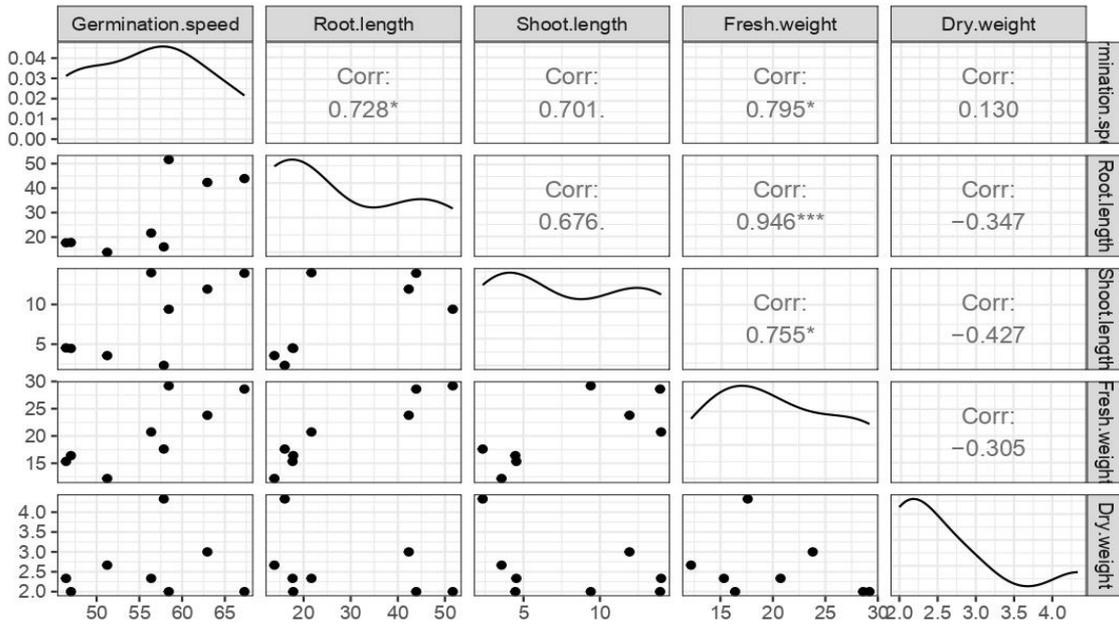


Figure 2. The correlation analysis among the studied traits in seed germination of *L. iberica*

3.3. Clustered heat map and principal component analysis (PCA)

The results of the heatmap analysis (Fig. 3) provide a clear classification of treatments into two distinct groups in terms of the incidence or absence of mannitol. The first group, which included treatments without mannitol, exhibited the highest values for germination speed, fresh weight, shoot length, root length, and RWC. This suggests that seeds germinated and grew optimally under non-stress conditions, where water availability was not restricted, leading to enhanced seedling vigor. Similar findings have been reported in studies on various plant species, where osmotic stress negatively impacts early growth stages by limiting water uptake and metabolic processes (Ru et al., 2022). In contrast, the second group, which included treatments with 100 mM mannitol, exhibited significantly lower values for most traits, except for dry weight. The increase in dry weight, despite the decrease in fresh weight, could be attributed to osmotic stress-induced dehydration, which reduces water content but does not necessarily impede the accumulation of structural biomass. Previous research has shown that mannitol-induced osmotic stress reduces cell expansion and elongation, leading to shorter shoots and roots as well as lower overall seedling biomass (Shah et al., 2021). The observed decline in RWC in the presence of mannitol further supports the notion that osmotic stress leads to water loss, disrupting cellular functions and growth processes. Studies have

demonstrated that reduced RWC under osmotic stress conditions correlates with impaired photosynthetic efficiency and lower metabolic activity, ultimately restricting seedling development (Farooq et al., 2012).

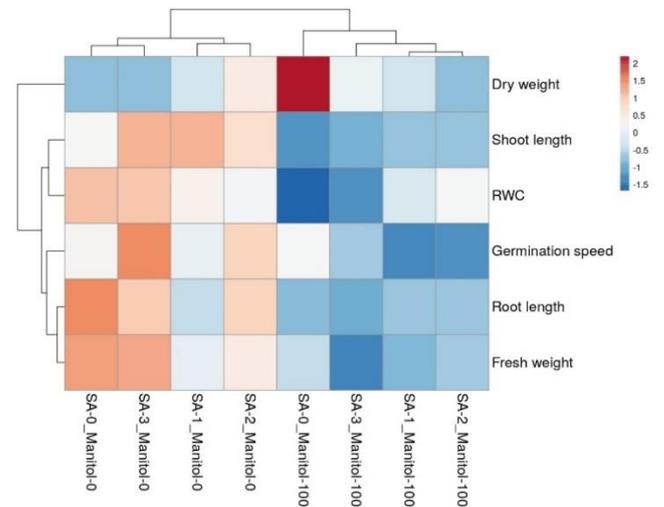


Figure 3. Heat-map cluster analysis of traits studied in seed germination of *L. iberica*

The results of the PCA provide insight into the morpho-physiological responses of *L. iberica* under drought conditions during seed germination, particularly when primed with the stress hormone of SA. The first two components of the analysis accounted for an impressive 91.5% of the total variation in the studied traits (Fig. 4), indicating that these components effectively summarize the majority of the dataset's variability. This significant proportion of explained variance suggests that SA plays a critical role in

enhancing stress tolerance in plants, including drought resistance. Numerous studies have also demonstrated the beneficial effects of SA application on germination speed and seedling growth under drought stress in various plant species, such as *L. iberica* and *L. royleana* (Sharafizad et al., 2013; Maleki Farahani et al., 2025). The dimensionality reduction observed through PCA, with just two components capturing major variations, further highlights the link between SA and modulating key physiological traits related to drought tolerance (Paravar et al., 2024).

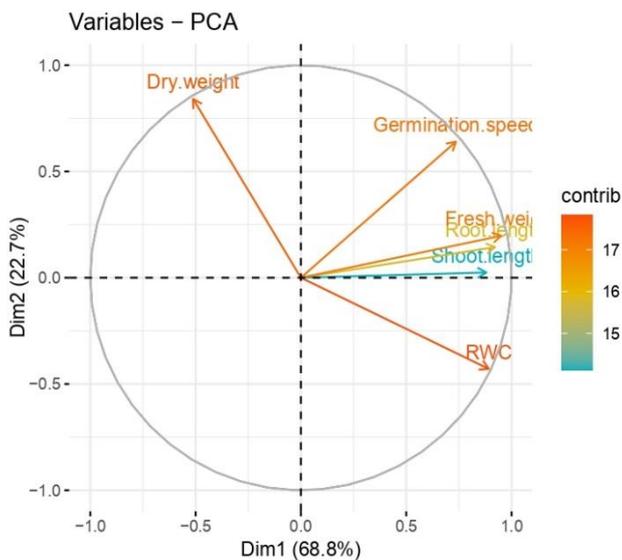


Figure 4. The bi-plot of PCA based on seed germination traits of *L. iberica* plant under drought stress.

4. Conclusion

The present study demonstrated that salicylic acid (SA) seed priming significantly influences the germination performance and early seedling growth of *Lallelantia iberica* under both normal and mannitol-induced drought stress conditions. The highly significant effects of SA, mannitol, and their interactions on all evaluated traits—such as germination speed, root and shoot length, fresh and dry weight, and relative water content (RWC)—underscore the pivotal role of these treatments in modulating early developmental responses in *L. iberica*. Notably, the application of 3 mM SA under non-stress conditions led to the highest germination speed, highlighting SA's promotive effect on early emergence. However, this benefit diminished under high osmotic stress (100 mM mannitol), suggesting a concentration-dependent and stress-contextual effect of SA. Root and shoot development, which are crucial for nutrient uptake and

light interception, respectively, were also found to be highly sensitive to mannitol-induced osmotic stress. The decline in RWC and fresh biomass under stress conditions further confirms the physiological limitations imposed by water deficit, which SA alone could not fully overcome. Correlation and principal component analyses reinforced the strong interdependence among key morphological and physiological traits, revealing that improvements in root length, shoot elongation, and water retention are tightly linked to overall seedling vigor. The clustering of treatments in heatmap analysis further confirmed that mannitol significantly alters the plant's response profile, emphasizing the value of SA priming primarily under favorable or moderately stressful conditions. Collectively, these findings suggest that while SA seed priming is a promising strategy for enhancing seedling vigor and partially mitigating drought-induced stress in *L. iberica*, its effectiveness is influenced by stress severity. Future research should include pot and field experiments to validate these findings under more complex and natural growing conditions, ultimately aiding in the development of robust agronomic practices for drought-prone environments.

Conflict of interests

All authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read and approved the final manuscript for publication.

Availability of data and material

All the data are embedded in the manuscript.

Authors' contributions

All authors had an equal role in study design, work, statistical analysis and manuscript writing.

Informed consent

The authors declare not to use any patients in this research.

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